

AD-A072 535

CALIFORNIA UNIV SANTA CRUZ CENTER FOR COASTAL MARINE--ETC F/G 6/3
BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN 'STENELLA LONGIROSTRIS--ETC(U)
JUL 79 K S NORRIS, T P DOHL

N00014-69-A-0200-7004

NL

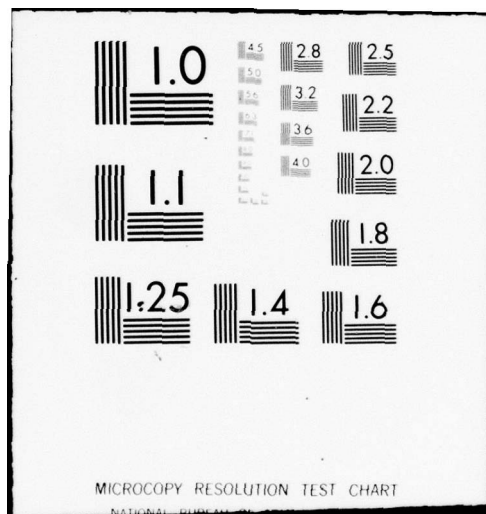
UNCLASSIFIED

| OF |
ADA
072535



END
DATE
FILMED
9-79

DDC



REPORT DOCUMENTATION PAGE

READ INSTRUCTIONS
BEFORE COMPLETING FORM

1. REPORT NUMBER		2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN STENELLA LONGIROSTRIS (SCHLEGEL, 1841).		5. TYPE OF REPORT & PERIOD COVERED Technical rept.	
7. AUTHOR(s) Kenneth S./Norris and Thomas P./Dohl		8. CONTRACT OR GRANT NUMBER(s) N00014-69-A-0200-7004	
9. PERFORMING ORGANIZATION NAME AND ADDRESS Center for Coastal Marine Studies University of California, Santa Cruz Santa Cruz, California 95064		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS	
11. CONTROLLING OFFICE NAME AND ADDRESS Ocean Science and Technology Division Office of Naval Research NSTL Station, MS 39529		12. REPORT DATE July 1979	
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) LEVEL		13. NUMBER OF PAGES 69	
15. SECURITY CLASS. (of this report) UNCLASSIFIED		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE	
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited			
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report) DDC RECEIVED AUG 10 1979 RLG/LLC			
18. SUPPLEMENTARY NOTES To be published in Fishery Bulletin, 1979			
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) 1. Dolphin behavior 2. Hawaiian Spinner Porpoise 3. Cetacea schooling behavior			
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) 411330			

AD A 072535

DDC FILE COPY

RECEIVED
MAY 24 1979

Office of Scientific Editor

021-FB

Rev. #2

Behavior of the Hawaiian Spinner Dolphin

Stenella longirostris (Schlegel, 1841)

Kenneth S. Norris and Thomas P. Dohl

Center for Coastal Marine Studies,

University of California, Santa Cruz,

Santa Cruz, California 95064

Accession For
NTIS GWA&I
DDC TAB
Unannounced
Justification

By _____
Distribution/Availability Codes
Available and/or special

Dist
A

79 08 08 031

ABSTRACT

The Hawaiian spinner dolphin, Stenella longirostris, was recorded from Kure Atoll to the island of Hawaii. It enters atoll lagoons or specific coves or swims over shallow sandy areas, usually near deep water, to rest. Access to nighttime feeding grounds may regulate the location of these rest areas. Rest areas are generally 50 m or less in depth.

()

¶ Natural scars and marks allowed study of movements and school structure. Schools are fluid assemblages of variable size and composition. Only small subgroups within schools may have long term integrity.

()

¶ Spinner dolphin exhibit several aerial patterns, including spinning which is mostly associated with sound production upon reentry, and each is typical of a specific school activity level. Sounds may serve as omnidirectional sound sources maintaining school cohesion beyond the limits of vision.

()

¶ The daily cycle of spinner dolphins consists of nighttime feeding, morning approach to shore, morning - midday rest, and travel to feeding grounds near dusk. Feeding is upon scattering layer fishes, squid and shrimp.

()

¶ Dolphins very commonly show scars from large sharks and from the small shark Isistius, which scoops disc-shaped pieces of blubber from them. These wounds heal to form dollar-shaped scars.

Introduction

fel. Most that is known in any depth about the behavior of dolphins has come from observations of captive animals. Yet the environment of captivity,

fel. which is at best a pool a few dozen meters in longest dimension and 5 or 10 ~~meters~~ deep, can allow only certain aspects of normal behavior to occur. Intragroup relationships may persist, but are usually distorted because relationships seldom remain intact. At best only hints of normal movement and activity patterns can persist where feeding schedules are determined by the workdays of trainers. In nature spinner dolphins, at least, travel constantly, even during rest. dolphins of many species dive and feed in very deep water.

Thus, however difficult it might be, the naturalist who would study dolphin behavior feels the need to study them in nature. It is usually no simple task. They are wary and travel many kilometers in a day. The presence of the observer almost inevitably causes bias. Dolphins hear exceedingly well, and dolphin schools may be aware of an approaching ship a kilometer or more away.

Our first ²~~two~~-year effort (1968-~~1969~~), with a spotted, or "kiko" dolphin school (Stenella attenuata), which we knew to frequent the area within a few kilometers of Kaena Point, Oahu, Hawaii, was abandoned for the reasons mentioned

- g
1. Kenneth S. Norris and Thomas P. Dohl
Center for Coastal Marine Studies,
University of California, Santa Cruz.

above. It simply proved too expensive of time, money, and effort to work with the animals. Our work was never free from observer bias. Reports of a school of spinner dolphins, ^(See 1941) (*Stenella longirostris*) living permanently in Kealahou Bay, on the Kona, or lee coast of the island of Hawaii, caused us to visit the area to see if work was feasible. We found an unusual situation in which several vexing observational problems were ameliorated.

Spinner dolphins do occur in Kealahou Bay frequently (our figures indicate occupancy about 74% of the time). The bay itself is remarkably good for observation. The Kona coast is normally quite calm, especially in morning hours. Lateral visibility is usually 20 m or more. The local people seldom disturb the dolphins. Only cruise boats, which seek out the schools and run through them, are a predictable disturbance. An abrupt 150 m lava cliff backs the bay. Schools sometimes came close to the cliff base at places where our visibility was blocked and could not be seen from the clifftop. But, most of the time we could watch wholly undisturbed schools at reasonably close range, although the distance proved too long for individual identification, and the lack of contrast between animal and background defeated good photography. Finally, the bay is relatively small, 3.2 km across its mouth and indented about 2.5 km deep. Its entire area was visible from the clifftop, and usually visibility was good enough that one could see schools well beyond its confines (Figure 1).

These unusual circumstances allowed us to gather new information about spinner dolphin behavior, especially about the diurnal cycle and patterns of movement, though some difficult observational problems remain.

Spinner dolphins proved exceptionally interesting observational subjects. Not only do they "spin," or leap from the water and revolve rapidly around their longitudinal axis, but they also perform other aerial behavior that can be observed from a considerable distance. These bits of aerial behavior, and the sequence in which they occurred proved to be a key to what one might call the emotional, or activity level of the school. This level in turn is closely correlated with a number of features of dolphin life, especially the regular sequence of activities during a daily cycle. Aerial behavior, once understood, become a predicator of daily activity patterns.

This work, performed in 1970-~~1973~~, presented represents a beginning analysis of natural spinner dolphin behavior, a field still in its infancy. Previous reports of the behavior of wild dolphin schools have been mostly single or very fragmentary observations (see Norris and Dohl in press for a review). A few detailed studies exist and allow comparison with this work, such as

the work of Saayman, Bower, and Tayler (Saayman ^{and} Tayler 1971; Saayman, ^{et al.} Tayler ~~& Bower~~ 1973; Saayman, ^{et al.} ~~Bower & Tayler~~ 1972; and Tayler ^{and} Saayman 1972), and more recently Würsig and Würsig (1977); Würsig (1978); Shane (1977); Wells, ^{et al.} ~~Irvine and Scott~~ (in press). Saayman and Tayler have analyzed the daily movements of ^{the} bottlenose dolphins, Tursiops aduncus, and the Indopacific humpback dolphin, Sousa lentiginosa, and their feeding formations and strategies for fish crowding and capture. Würsig's studies concentrate on Argentinian populations of Lagenorhynchus obscurus and T. truncatus, while Wells Irvine and Scott's work deals with T. truncatus in Florida.

There are parallels in these works with the behavior patterns described here. The recent work by the Würsigs on the group size, composition and stability of bottlenose dolphins schools bears similarity. Like ours, much of this work was performed from clifftop observation posts using natural scars and marks to identify individuals. Shane's study, also on bottlenose dolphins utilized natural scars and marks. Wells et al, carried out extensive tagging studies on Florida bottlenose dolphins. All of these studies and that reported here show remarkable fluidity in school composition and size over short periods of time. The dolphin populations that have been studied, it seems, are not composed of discrete schools of modest size but instead of highly fluid groups that may range considerable distances and may be found associated in very variable combinations of individual animals.

Morphology. Hawaiian spinner dolphins are moderate-sized, slim-bodied, and long-beaked odontocete cetaceans. Adults reach at least 2 m total length, and about 55-62 kg (Perrin 1975). They are handsomely marked animals with a dark gray cape over the dorsal surface, a light gray lateral field (using the terminology of Perrin 1972) sharply demarcated from the cape above and the white belly below. (Figure-2) The white of the belly extends up the flanks to about the level of the eye. The beak, or rostrum, is dark gray, tipped prominently with black, the lip margins are dark and the ventral surface of the beak is white. The pectoral fins are dark gray, and a dark flipper band connects its anterior insertion to the eye, which is surrounded by a black eyepatch. Flukes and dorsal fin are dark gray. These color pattern components have been described in more detail by Perrin (1972), and they have been compared to patterns of geographical forms of spinners living in the eastern tropical Pacific. In nature, against the blue or turquoise backdrop of tropical water, the dark pattern components of spinner dolphins appear in shades of brown, but the effect is usually lost when the animals are removed from the water. The white and other pattern marks are often suffused with pink, from superficial blood flow in the blubber, which may also contribute to the overall brownish cast of pattern components in living spinners.

Systematics. In recent years a worldwide picture of the distribution and systematics of tropical odontocetes has begun to emerge. Well-documented collections, often with measurements and photographs, have been made from all oceans, especially where dolphins are involved in fishery operations (Perrin 1975; Kasyua, Miyazaki and Dawbin 1974). A special

beneficiary of this work has been the once chaotic genus Stenella. It now seems reasonably clear that the genus is composed largely of three major species or species complexes: the spinner dolphins (allied to Stenella longirostris of the Hawaiian Islands), the striped dolphin (Stenella coeruleoalba), and the spotted dolphins (allied to Stenella attenuata of the Hawaiian Islands). All are tropical or subtropical. All are often found far offshore, or near islands.

In the eastern and central Pacific Perrin (1975) discerns four geographical forms of spinner dolphins a Costa Rican long-snouted form occurring close to the Central American coast, an Eastern form occupying the open sea from the American coast out to 115° W longitude, a Whitebelly form occupying the open ocean both south and west of the Eastern form (and overlapping with it to some extent) to about 145° W and nearly to 5° S latitude, and an Hawaiian form, localized around the Hawaiian island chain. Perrin (1975) states that Hawaiian spinner dolphins are most closely related to the adjacent whitebelly form, differing from them by being somewhat more robust, by having a larger area of white belly coloration, and by lacking the speckled margins of the white belly field. He places the complex tentatively in the species Stenella longirostris.

Most of the races of spinner dolphins from around the world are quite similar to the Hawaiian form. Only the Costa Rican and Eastern forms are strikingly different, being nearly uniform gray in coloration, with faint hints of pattern components found in other races. These aberrant forms also show remarkable sexual dimorphism, which is otherwise rather subtle throughout the species. Fully adult males of these two races often possess a dorsal fin that is canted sharply forward, "like it was stuck on

backward" and a very heavy post-anal protuberance. The fin of Hawaiian spinner dolphins is either triangular or very slightly falcate, and only a subtle post-anal protuberance can be noted in adult males.

Methods

A camp was established on the Greenwell Ranch at the edge of the cliff overlooking Kealahakua Bay (Fig. 1). Two observation sites were used for recording and observation by telescopic means. Observer teams kept regular watches during daylight hours.

Several vessels were used for observations at sea, or to provide an anchored platform in the bay, including the brigantine Westward and the motor sailers R/V Hikino, and the R/V Imua. A trip through the northwest Hawaiian chain was made on the Coast Guard buoy tender Buttonwood.

Fourteen spotting flights were made throughout the main Hawaiian chain, mostly from small fixed wing aircraft.

Underwater observation used a specially built underwater observation vehicle or mobile observation chamber (MOC) 6 m long which looked like a small submarine (Fig. 3) but did not submerge. It consisted of a float made from an auxiliary aircraft gasoline tank and a central observation chamber. The viewer in this chamber below water obtained ventilation from a squirrel cage blower, and was surrounded by a band of plexiglas windows at eye height. Controls for turning or tilting the draft were at hand, and a tape recorder was connected to a

hydrophone¹ mounted amidships and oriented forward.

The craft was run by an outboard engine set in a well aft. Stability was maintained by 900 kg of lead blocks in a compartment below the observer's feet.

Other underwater observations were made with scuba, or by putting an observer with snorkle or scuba below the bow of a slowly moving skiff, holding onto a bow painter. In this way observers could sometimes be towed among the animals, and even be jostled by them. A field station was established at the village of Napoopoo on Kealakekua Bay.

Feeding was observed from skiffs and larger vessels. Dipnet samples were taken in the region of feeding, and stomach analysis of such specimens as became available to us were collected. The squid and crustaceans in stomach samples were identified by Richard Young of the Department of Oceanography, University of Hawaii. Fish otolith collections were lost through improper preservation.

Recordings were made with a hydrophone deployed from a stationary skiff located near a school of animals, or from the MOC Monitoring was by use of headphones. During our studies we were fortunate to have William Schevill and William Watkins of Woods Hole Oceanographic Institution establish a four-hydrophone array deep in Kealakekua Bay. With this apparatus, three-dimensional tracks of passing porpoises were obtained that were of greater range and fidelity than allowed by our simple gear. The

¹An Atlantic Research Corporation LC 32 hydrophone, a Hewlett-Packard 466A preamplifier, and a Uher 4000s 1/4 inch tape recorder comprised the recording gear. The upper frequency response of this system was approximately 20 kHz at 7 1/2 ips. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

experimental arrangement of this array and recording characteristics is described in Watkins and Schevill (1974).

Porpoise radio tracking used dolphin dorsal fin
radios (see Evans 1974) and a hand held direction finder. Dolphin
capture used a standard head net.

Throughout this paper we use the term "school" to indicate all animals in a discrete area that move together. Such schools are often composed of recognizable, discrete "groups" of animals clustered together and moving and diving more or less in unison. For instance, while the direction of movement of larger schools may be the same for all its parts, diving synchrony for all animals may be quite extended and ragged, being composed of a number of synchronously diving groups. Within such groups one can sometimes recognize small "subgroups" of a few (2 to perhaps 12) animals that are often seen together, regardless of the group or school composition around them.

Distribution

Marine mammal collectors of an Hawaiian oceanarium, Sea Life Park, suggested that spinner dolphins occur habitually at certain areas along the island shores, while they are largely or wholly absent from others. This led us to collect sighting and capture locations for the entire Hawaiian chain. The same collectors reported that after collection of animals from a given school, the school as a whole might become shy of the boat for an indefinite period, and suggested that it occupied a given area of coast and the the school might have integrity through time.

We found that spinner dolphins occur throughout the Hawaiian chain, from its northwesternmost limit at Kure Atoll (lat. $25^{\circ}40'N$, long. $175^{\circ}38'W$) to its southernmost limit at South Point, or Ka Lae, on the island of Hawaii (lat. $18^{\circ}49'N$, long. $155^{\circ}41'W$). Occurrence is not random, but spinner dolphins are gathered in small to moderate schools (6 to about 250 animals) near all major islands and shoal areas, and can be found with some regularity near certain shoals or coves. Only near small islands that drop abruptly without having significant shoals, such as at Nihoa Island, have we not found spinner porpoises. The following is a synopsis of known spinner distribution. Unless otherwise specified, all sightings were by the authors. Specific records are shown in Figure 4.

Kure Atoll. On September 3, 1971, Norris visited Kure Atoll. The commanding officer, Lt. (j.g.) Joel Greenberg, reported having seen a school of 20-30 spinner dolphins enter a west pass into the atoll lagoon. Without prompting he described spinning behavior.

Midway Island. On the mid afternoon of September 3, 1971, a school of approximately 35 spinners was noted in shallow water at the edge of the channel inside of Eastern Island. The regular daytime occurrence of animals in the shallow atoll lagoon was reported, to us by residents of Midway.

French Frigate Shoals. September 12, 1971. At 0830 hrs 30 animals were noted just off Shark Island, spinning and leaping.

Pearl and Hermes Reef. Edward Shallenberger reported seeing, a spinner school at this location in the fall of 1978, entering the central lagoon during the day.

Necker Island. 10.2 miles ESE of Necker Island at 1600 hrs a school of approximately 30 spinners was noted.

The following localities in the northwest Hawaiian chain were visited without seeing spinner dolphins Salmon Bank, Lisianski Island, Laysan Island, Gardiner Pinnacles, and Nihoa Island. Five to 10 animals that may have been spinner dolphins were seen 18.5 miles, 134°T from the wreck at Maro Reef, by Ensign Albert Sarra USCG, on September 9, 1971.

Niihau Island. Spinner dolphins have been sighted at Kaumuhonu Bay (60 + animals) at the southwest tip of the island, between Lehua Island and Kikepa Point (20+ animals), smaller schools (15 + each) have been noted along the southeast shore near Pueo Point, and on the northwest shore at Nonopapa. The Nonopapa record was of a travelling school that moved close to shore along perhaps half of the northwestern coast.

Kauai Island. Spinner dolphins schools were found around the island at 3-16 km intervals, except along its western coast. The largest schools were estimated at 150 animals on the Napali Coast, a 70-80 animal school just north of Kahala Point, and an estimated 60 animal school between Hanapepe and Kaumakani. Smaller schools, scattered along the south and east coasts averaged about 15-30 animals. The only obvious difference between the vacant coast and the occupied areas is that vacant areas have much narrower shallow water shelves devoid of deep indentations in the coastline.

Oahu Island. Records from various sources over 14 years (1962-1976) show that two broad areas of the coast are nearly always occupied by spinner dolphin schools during the day. First, along the Waianae Coast between Barber's Point and the vicinity of Kaena Point (the west or Kona shore) schools estimated between 30-100 animals can nearly always be found close to shore during the day. Second, an apparently larger school or schools is often seen in the coastal area between about Pearl Harbor and Makapuu Point.

Schools of animals seen in this area have been estimated to number from 40-250 individuals. Small schools have been seen near Kahana Bay and Waimea Bay. Because this is the windward coast, subject to almost constant tradewinds, little collecting effort has been expended there and dolphins may be more common than our records indicate. A relatively narrow shelf (1.6 km) exists along the Waianae Coast except at Kaena and Barber's Points where it broadens considerably. The shelf around the remainder of the island is much broader, averaging about 4 km and is marked on the northwest and northeastern coasts by a fringing reef.

Molokai-Lanai-Kahoolawe-Maui. Geologically this four-island complex has resulted from one series of volcanic eruptions, producing islands with inter-connecting shallow areas and channels. Spinner schools have been seen at several locations around the margins of this complex, but seem rather seldom to travel to inshore locations over extensive shallow areas such as that at Lahaina Roads (Auau Channel), or over the flats between Molokai and Lanai Islands (Kalohi Channel). Dolphin schools in such areas would have to travel 11 km or more from deep water to reach these shorelines.

Large spinner schools have been seen over Penguin Bank (between western Molokai and Lanai Islands), the south coast of Lanai, especially near Manele Bay (40-100 animals), along the south shore of Kahoolawe, especially near Halona Point, small schools on the north Molokai shore at Kalaupapa and Cape Halawa, and small schools along the Hana Coast of Maui, and at Lipoa Point on the northwest end of Maui. Two records of spinners accompanying humpback whales near Lahaina were reported to us. Bottlenose porpoises Tursiops sp. have often been seen with these whales.

Hawaii Island. Spinner dolphin schools have been found at scattered locations around the entire periphery of the island except for the

northeast shore, though there are some shorter stretches of coast where we have never seen schools. It is not surprising, in view of the large size of this island, that there are more localities of regular occupancy by porpoise schools than for any other island. We found ²¹ areas of regular occupancy and ⁴ localities with more transient occupancy.

On the lee side of Hawaii, the largest school was centered at Keahole Point, ranging along about 23 km of coast, from Honokohau Harbor to Kiholo Bay. In all, there are estimated to be about 200-250 animals generally occurring in this area, and they may be found in a single school at times, or fragmented into two or three smaller schools, separated by a few kilometers of coastline. Here, the dolphins do not seem to occupy any of the small coves consistently, but to congregate over the rather extensive area of shallow water, moving back and forth. Not uncommonly, parts of this aggregation moved during the day beyond the limits listed above and may move as far as Kailua-Kona or beyond, though the constant sea traffic in that harbor seems to prevent normal daily quiescence (defined below). We have termed these animals collectively the "North Kona School." Twenty-eight km to the south, at Kealahou Bay, a school ranging from 2-70 animals (average 25 animals over 73 observations) was found. In our observations dolphins occurred in this bay on 74% of 113 observation days. They most commonly occupied the deeply indented bay but sometimes were found on the shallow area north of the bay to Keauhou, or occasionally nearly to Kailua-Kona. Less commonly they were found to the south in or near the very small bays at Honaunau (City of Refuge) or Hookena.

The entire 56 km stretch from Hookena to South Point seems not to harbor spinner dolphins schools on a regular basis, though it should be

noted that a military air closure zone prevented our flying over the Milolii area regularly. We have a single record of a 20-animal school at Milolii. This precipitous coast drops abruptly into deep water, without shallow areas alongshore. Much of the coast is composed of relatively new lava flows from nearby Mauna Loa volcano.

Small schools, estimated generally at about 20 animals were seen, usually in very rough water, at South Point, between Ka Lae and Honuapo, over the modestly developed shallow area there, or occasionally in the deep cove at Kaalualu.

At Keauhou Cove, directly below Kilauea Crater, a small school (20-25 animals) was consistently found. The dolphins came into very shallow water there in an area protected by Keaoi Islet and flanking coral heads, which produce a small area of calm water along an otherwise rough water coast.

Cape Kumukahi, the easternmost point on the island, hosted a population of about 30 animals. Several small irregular bays along the southern edge of the Cape form the "home bay" in this area, with animals being noted at times as far as Opilukao Cove.

The largest school on the windward shore (ca. 100 animals) was often found at Kaloli Point, 18 km south of Hilo Bay. This location seemed also to be the northernmost area of occupancy on this side of the island. The dolphins were typically found in the bay protected by the point and fringing coral reefs. The rather shallow bay (maximum depth 20m) is close to deep water to the south.

The 112-km stretch of coast from Kaloli Point to the north end of the island (Upolu Point) seemed devoid of resident spinner dolphin schools. It is also the site of the major sugar cane processing plants on the island.

Effluent from these plants seems to produce murky waters along the coast and clearly contributes to the long drift lines of flotsam from processed sugar cane. Whether the absence of animals and this activity are related is unknown.

At the north tip of Hawaii we occasionally saw or heard of small schools of spinners (10-30 animals) in the area between Kawaihae Bay and Honoipu, though more often the entire stretch of coast was found to be without animals from about Kihole Bay to the north tip at Upolu Point. This circumstance is anomalous, in that well developed shallow water areas occur along this shore, where schools might come during the day, and where the sea is generally calm.

Rest Areas

Three features of the distribution of spinner dolphins in the Hawaiian chain stand out. First, the distribution is discontinuous. Some coasts may have several areas where dolphins congregate, and others may have stretches of many kilometers in extent where no animals are seen. Second, certain coves or shallow areas are clearly regular aggregation sites, while others seem to be used much more infrequently. Third, some areas consistently carry more animals than others. As we will demonstrate, spinner dolphins come inshore during daylight hours to enter a quiescent period of some hours duration, and we think of these congregation sites alongshore as "rest areas."

What typifies such rest areas? First, all rest areas are shallow sandy areas with less than 50 meters depth over part of their extent. They are usually composed of a mixture of open sandy bottom dotted with coral formations. Coves may or may not be present. All rest areas are close to deep water. Usually water in excess of 500 meters depth can be reached within a

few kilometers. Some schools, such as those in the Waikiki (Oahu) or Manele Bay (Lanai) areas, have access to considerably shallower water than others. Schools living there may be restricted to waters no deeper than about 600 meters, since our observations on the Kona coast of Hawaii indicate that schools do not move more than a few kilometers from shore at night. Other schools, such as at Keahole Point (Hawaii) regularly move into water in excess of 2000 meters depth. Of course, the observations we have made on the island of Hawaii may not hold elsewhere.

Apparently spinner dolphins only occasionally travel far onto extensive shallow areas like that at Lahaina Roads (Auau Channel), which is about 24 kilometers in length. Instead they typically congregate along its margins, along the south shore of Lanai Island, and Kahoolawe Island, where deep water is nearby. The areas most closely studied here, Kealakakua Bay and Keahole Point both have deep water accessible within 1.5-2.5 kilometers of shore. The inference is that rest areas are chosen by dolphins not only for physical characteristics such as depth, bottom type and perhaps calm water, but also for their accessibility to nighttime feeding areas.

Spinner dolphins schools also rest in atoll lagoons. At Kwajalein Atoll, on September 10, 1973, at 1630, a school of about 40 spinners was noted about 1 km inside Bigej Pass. The school was moving toward the pass, presumably on its way out to sea. A local resident told us that the school was regularly in this pass, and not found in other nearby passes into the central lagoon. Similar observations have been made at Kure Atoll, Midway Atoll, and near Shark Island at French Frigate Shoals. The animals (approximately 35) resting quietly in a shallow channel not far inside Eastern Island at Midway, were sighted from a helicopter. Probably wherever atolls and spinners dolphins occur together the animals use the atoll lagoons for rest.

In the eastern tropical Pacific a large spinner population occupies oceanic areas far from land. In view of the use of shore situations elsewhere in the range of the species, one wonders what, if any, substitution is made. Norris and Dohl (in press) have speculated that the frequently observed association between spinner and spotted dolphins (Stenella attenuata) in the eastern tropical Pacific (this association does not occur in Hawaii) may hold the answer. Spinner dolphins may seek the schools of spotted dolphins for refuge during rest in the open sea. We believe this may be true because spotted dolphins feed during the day, while spinners are nocturnal feeders and spinner dolphins schools have been observed to join spotted dolphins schools in the morning (Norris et al. 1978).¹ If such rest association occurs the spinner dolphin are associating with alert animals in this oceanic area. Related to this the yellowfin tuna seine fishermen chase and encircle dolphins to catch tuna, most fish apparently follow the spotted porpoise. Since the association between tuna and dolphin is probably food based the fish may be following the dolphin species that is actively searching for food. That is, like the tuna, the spinner dolphins may follow active dolphin schools.

Spinners resting along shores maintain a continuous but slow locomotion, and it seems likely that the searching or feeding activities of spotted dolphins would not greatly change these requirements for rest.

Marked Animal Studies

Dolphin schools are seen frequently at the same localities while other areas never seem to harbor them. Are these schools of resident animals, or are they composed of transients that for some reason choose certain regions of the coast for rest? The frequent observation
¹Norris, K.S., W.E. Stuntz and W. Rogers 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna industry-preliminary studies. Final Report No MMC76/12 PB 283-970 Nat. Tech. Inform. Service. xi + 86p.

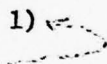
of porpoise collectors that a given school will avoid their vessel after animals have been collected from it (Norris and Prescott 1961) indicates possible residency. On the other hand, dolphin schools are not always in these rest localities, and the number of animals using a given cove may vary widely from day to day. This indicates fluidity in school structure, and variability of school movement. Such fluidity has been noted for other porpoise schools by Würsig and Würsig (1977), and Saayman and Tayler (in press).

Because we were concerned that the spinner dolphins of the Kona coast of Hawaii not fear our vessel, we sought to recognize individuals by natural scars and marks rather than by placement of tags. Ultimately we were able to catalogue 50 recognizable individuals and resightings provided a partial picture of school and individual movements. Our shipboard work with dolphin schools was restricted almost wholly to Kealahou Bay through most of 1970. Only toward the end of that year and during 1971 and to a limited extent later, was much sea time spent in other areas. Hence a large proportion of our sightings do not bear on the question of dispersal distances or rates by individual dolphins. We gathered information on possible inter-island movements.

By far the most useful scars and marks were those of the dorsal fin. Twelve of our animals were in this category (Fig. 5). These animals could be resighted from shipboard, and sometimes from considerable distances. It is not surprising that the most (49, or 64%) of our 76 resightings were of these animals.

Many marked animals had scars or pattern peculiarities. Such marks could only be sighted on dolphins at the bow of the observation vessel, or

from our underwater viewing vehicle (MOC) . The MOC was used sparingly because it was noisy and disturbed dolphin schools, and because it was safe only in calm seas. Thus, information on repeated social associations within schools is limited to two sets of sightings and journal notes over 14 days, all within Kealahou Bay. In any school only a few individuals seemed to swim at the bow of a vessel, while others stayed well clear, thus reducing the chances of sighting many animals. Of 38 animals catalogued with body scars or marks, there were 27 resightings. The final marked animal recorded was an individual with a vertical white stripe on its dorsal fin (Fig. 5).

Our store of recognizable animals built up slowly over the entire period of the study, thus making interpretation of movements difficult. Nonetheless, some important ideas emerge: 1) 

No resident school permanently and regularly uses a given cove or local region of shoreline. Instead, each cove or resting spot may harbor a given subgroup of dolphins for a matter of days or weeks. 2) Schools are labile mixtures of groups and subgroups. 3) Individual movements may span the entire Kona coast, or even beyond (true ranges of movement remain unknown). A few "marked" individuals have been seen over rather long periods, but other equally recognizable animals have been seen only briefly, or never again after an initial sighting, suggesting either rapid population turnover, or high levels of intermixing between the various schools of the area.

Two pale animals were seen. They were very different visually from their associates. This was especially evident from the air. They were seen along the entire southern Kona coast from Keahole Point to Kamilo Point east of

Ka Lae (South Point), and over the longest time span for any "marked" animals (1220 days out of the total 1246 day recording period). These pale animals were seen either alone, or on occasion together in the same school. These data are suggestive only, because such pale coloration cannot be assigned definitely to a given animal since it is a recurrent condition in the species. For example, such a pale animal was captured near Oahu, and for some years was an exhibit animal at the oceanarium Sea Life Park. The animal, called "haole" for "white person," gradually grew darker during captivity but always remained a slightly pale. Perrin (1972) described

a pale animal from the eastern tropical Pacific, as "albinistic."

Let us examine each of our conclusions in turn. First, is the question of residency. Taking only those animals recognizable from the surface, we find that 7 of 12 animals were seen in both the large Keahole Point schools and in the smaller Kealahou Bay schools. The pale animals were seen both in Kealahou Bay and Keahole Point schools, and far to the south at Kaula Point. There were long periods when a given animal was not seen at one or another locality. This information cannot be usefully quantified because schools were sometimes large and all animals could not be examined, and because our records are not the result of concerted attempts to check each animal in a given school. Instead, the records reflect opportunistic sightings during the pursuit of other activities.

Animals clearly moved back and forth between the Keahole and Kealahou Bay assemblages. Of the 12 animals, six were seen at more than one locality and then returned to the first locality of sighting at least once. Three animals were seen at a single locality only, but this may reflect low sighting frequency rather than lack of movement.

Finally, three animals were seen at two or more localities but did not return to the locality of first sighting. For these reasons we reject the idea of a given cove having a definable resident school (Table 1).

Our data are too incomplete to show how long a given animal might spend at a single locality, or how often it switches between rest localities. Only the number of consecutive days during which a given surface-visible marked animal was seen at a single locality vs. the number of days of consecutive observation during the sighting period is indicative. Considering the animals for which most resightings are available: numbers 24 and 30, during four separate continuous periods of observation of 9, 8, 9 and 10 days, animal 24 was seen 2, 2 and 3 days consecutively (Table 2). Animal 30 was seen only once, 2 days in a row, during consecutive observation periods of 7, 10 and 10 observation days. Animal number 13 (a large calf traveling with its mother) was seen three consecutive days during a 16 day observation period at Kealakekua Bay. During consecutive observation periods in which the observer moved from Kealakekua Bay to Keahole Point, certain animals were noted on consecutive days at the two localities, indicating a switch in a single night from one to the other. These data indicate that movements are frequent, at least between the Kealakekua and Keahole rest areas.

As for the conclusion that dolphins schools consist of labile aggregations of groups and subgroups, the best information comes from fluctuations in school sizes with which a given marked animal was associated. The results reflect almost the entire range of school sizes observed. For example, at various times number 24 was found in schools varying from 7-10 to 120 animals, and number 30 covered approximately the same school size range: from 6 to 150 animals. Observations from the MOC showed that on one occasion the same

subgroup, with the same general internal arrangement of animals persisted for at least three days. Many times, during three consecutive observation days (March 25-27, 1970) the same subgroup of five animals came to the bow of the MOC. This sort of association is well known in captive schools and persists for long periods of time (McBride and Hebb 1948, Tavalga and Essapian 1957, and Bateson, See Footnote, P. 00). Such groups in captivity may be constructed of related or non-related animals or even of animals of different species (Bateson 1965). Thus, while our observations of wild schools do not provide proof, we expect that some subgroup structure may persist over long periods and that familial lineages may be important, as has been observed in captivity (Tavalga and Essapian 1957).

The role of subgroups in larger schools is apparently not simple. Such schools are not simply composed of groups and subgroups that themselves have cohesion. Instead, there are also some assemblages that seem typical only of large schools. For example, in large schools, groups are often segregated. Groups of juvenile animals, or of mother-young pairs may be seen. Large schools differ from one another by the presence or absence of such groups. Some schools were composed only of adults, while others had a high proportion of young animals. Subgroups may move between schools. Some social ordering largely related to growth and reproduction, may take place in schools regardless of the origins of their constituent parts. A major force in such ordering within large schools may be the aggression of certain large adults, that may be either male or female, who herd vulnerable groups to central locations within the school (see McBride and Hebb 1948). Such patterns have been proposed for Stenella coeruleoalba by Kasuya (1972) and for S. attenuata by Kasuya, Miyazaki and Dawbin (1974).

Behavior Patterns

Aerial behavior. An experienced observer of spinner dolphins can quickly judge the activity state of a school by watching its aerial patterns. It is possible to judge the alertness of school members by checking the kind and frequency of aerial patterns. In fact, such analysis soon makes it obvious that the entire sequence of changing behavior patterns through any 24 hour cycle is related to the level of activity, or "emotional state" as indicated by aerial patterns.

Spinner dolphins not only "spin" but perform several other clearly recognizable aerial patterns. These include leaps, head-over-tail leaps, backslaps, headslaps, noseouts, and tailslaps, or a combination of these patterns-- each performed with variable vigor and frequency at various times of day:

1) The Spin. The dolphin rushes to the surface as if about to make an arcing leap, and at the last instant, when most of its body is out of water, tips its flukes slightly and flexes its tail stock, causing the airborne animal to spin about its longitudinal axis. As many as four revolutions may be made in the course of such a leap (Hester, et al. 1963). The dolphin may literally appear to flicker as flippers, flukes and the dorsal fin flash by. The animal falls back into the water, usually partly on its side, and its rapidly rotating body scoops out a hollow of water around the sinking animal. The hollow then collapses producing a welter of spray and a discernible clap of sound (Fig. 6). The spin is enhanced in air by postural movements, in addition to the momentum initially imparted when leaving the water. Just as a gymnast flexes his or her body or as a skater moves elbows in a spin, the spinning

dolphin flexes its head and tail, and moves its flippers toward or away from its body (Fig. 7).

Spins are usually performed in series of descending intensity (as are other aerial patterns). A given animal may spin as many as a dozen times in succession, each successive spin generally being of somewhat reduced intensity compared to the last. The first leap may reach an apex perhaps 3 meters above the surface, while in the last of a series the animal may not clear the water at all. Most spin series are short, being composed of three or four spins.

All age classes spin. It is not uncommon to see small calves spinning repeatedly in moving schools. In one case a young animal leaped into a spin while in a feeding school, landing a dozen meters off our bow. Each successive spin brought the animal closer to us, as it was seemingly oblivious of our presence. The last spin launched the animal nearly at the bow and it fell back into the ship's bow wave, startled and swam rapidly away below the surface.

Spins may be seen in all parts of a school. Leadership or dominance do not seem to be obvious factors in spinning behavior. In fact, the opposite could be true since very young animals spin and in our observations of captive spinners a high frequency of spinning was observed in an animal that had not been socially accepted into the resident captive school. The best correlation of frequency of spinning and the condition of a school seems to relate to alertness, or activity level of the animals involved; the greater the alertness the more frequent the spins. The more spread out a school the more frequent spins

seem to be. In feeding schools, which are the most dispersed of all school formations, spinning and other high energy aerial behavior occurs almost continuously.

2) The Leap. The most common aerial behavior in which spinner dolphins actually leave the water is the leap. Spinners perform leaps by bursting from the water at about a 30° angle, rising a meter or two about the surface, and falling back into the water on the belly or side in a welter of foam. Less frequently, reentry may be made cleanly, snout first.

3) The Tail-over-head Leap. The most active and perhaps physically demanding aerial behavior pattern is the tail-over-head leap, and its variant, the tail-over-head leap with a spin. These aerial patterns are seen only when the school is most active. In this pattern the animal bursts from the water at a rather high angle, slings its tail over its head in a wide arc, usually trailing a spiral of spray and enters tail first, often slapping its flukes against the water with a loud "thwack" in the process (Fig. 8). On occasion this may be accompanied by one or two revolutions of a spin at the same time.

4) The Backslap. The animal leaps about half or a little more of its length out of water at about a $30-45^{\circ}$ angle, upside down, and as it falls back it arches its body sharply, giving the water a sharp slap with the dorsal surface of its head and beak (Fig. 9). Backslaps are often performed in slowly moving schools.

5) The Headslap. The reverse of the backslap, and the animal emerges in the normal position, once again at about $30-45^{\circ}$ to the water surface and then flexes its head sharply downward, slapping its chin and lower beak against the water (Fig. 10). It is one of the most common patterns seen in moving schools.

6) The Noseout. The least active aerial behavior. The dolphin simply arches its back as it swims to the surface, raising its snout into the air. It is sometimes seen briefly when a resting school is disturbed, or in schools where other, more active behavior is occurring. It is often the first aerial behavior seen in an awakening school.

7) The Tailslap. This pattern may be performed in either the normal or the inverted position. With the dolphin at the surface the tail is arched, bringing the flukes above the surface. They are then brought down smartly against the water producing a clearly audible sound. In the inverted position an animal may sometimes scull along making repeated and rapid tail slaps in a behavior we have called "motorboating," because it not only leaves a continuous wake, but makes a "pop pop pop" sound. An animal may slap 10 to 20 or more times in succession in this way (Fig. 11). A whaler's term, "lobtailing," describes the same behavior, but seems less descriptive than "tailslap," a term now widely used by porpoise trainers.

What are the functions of aerial behavior? A key point, we feel, is that each pattern, with the possible exception of the noseout clearly makes noise, and in fact seems primarily structured to make noise. For example, in a headslap the last component of the pattern is a rapid flexure of the trunk and neck causing the chin and throat to slap against the water. The tail-over-head leap effectively slaps the flukes against the water with great force. The spin scoops a cavity from the sea surface whose walls collapse and thus produce a sound we have heard both above and below water. Other aerial patterns are similarly structured. Such sounds probably radiate in all directions. Dolphin sound generation and beaming apparatus, on the other hand, transmits sound in a structured beam, directed

forward (Schevill and Watkins 1966, Norris and Evans 1967, Evans 1973). This beaming is better known for clicks than whistles or burst pulse signals, though apparently also true of the latter, at least in the killer whale, Orcinus orca (Schevill and Watkins 1966). The directionality of clicks has been discussed for S. longirostris by Watkins and Schevill (1974). Thus, while vocal signals are directed almost wholly in certain sectors, the sounds of aerial behavior are likely to approach omnidirectionality. Our recordings indicate that none of the signals of aerial behavior propagate long distances. Tail slaps may be the loudest.

Aerial behavior is most frequent in fully active schools in which the animals are dispersed, sometimes rather widely. In tight resting schools (see below) sounds of all kinds except for desultory clicking are nearly absent. Conversely, our observations of a captive spinner dolphin school held in a community tank at the Oceanic Institute, Oahu, Hawaii, showed that aerial behavior continued through the night, and in fact was most frequent in the dark. Thus, high frequencies of aerial behavior seem correlated with conditions in which many animals in the spread school cannot see each other.

Finally, these patterns are stereotyped by species, and a trained observer can often visually identify the genera or species of dolphins by their aerial patterns, sometimes from long distances. Perhaps the dolphins can make such identifications underwater, by sound.

What can the use be of such sound signals? The following possibilities seem apparent: 1) If we can gauge the activity state of a school by its

aerial behavior it is likely that the dolphins can do so too, and probably in a more refined way than we can; 2) such sound signals may be used where vision is useless; 3) school cohesiveness in the dark, or when animals are spread beyond the limits of vision, may be promoted by repeated short range omnidirectional sound signals from all parts of a school. The incidence of aerial behavior is correlated with times when such signals would be most useful. This seems to us to be the most likely function.

We considered, and rejected the idea, that the spin might be a pattern relating to dominance or courtship in the school. This seems refuted because animals of all age classes and both sexes spin, and because captive observations have shown that even animals that have been rejected from the social structure of a school spin.

Another possibility is that spinning is related to removal of ectoparasites such as remoras and copepods. While it might be useful occasionally in detaching such creatures we have never seen a case in which this seemed to be occurring, and essentially every animal observed to spin was apparently without such parasites. Captives spin regularly even though free of parasites.

The Daily Activity Cycle

Observations of spinner dolphins schools along the Kona Coast of the Island of Hawaii, and to a minor extent elsewhere in the Hawaiian chain, show a regular sequence of activities during each 24 hour period. Broadly, this consists of nighttime feeding, about which we know little, morning coastward movement that brings the animals into coves and sheltered coastline areas, rest, awakening, zig-zag swimming, and then departure to the feeding grounds. Each of these activities will be discussed in turn.

Feeding. Feeding is upon scattering-layer organisms, (Table 3) and seems to be performed during synchronous or subsynchronous dives of large and dispersed schools. What we take to be feeding dives start as early as dusk, before most of the scattering layer approaches the surface, and such evidence as we have (mainly from a single radiotracking, from chance encounters with schools at night, and from schools that we have followed to the feeding grounds) suggests that the schools patrol along breaks in the submarine island slope, and toward morning gradually make their way into shallow water over the shelf.

A radiotracked animal, caught over approximately 140 m of water at Keahole Point, Hawaii just before dusk (1650 hours) on March 1, 1971, moved back and forth along the shore between a point near Kailua-Kona and Kiholo Point. A detailed radiotrack was made during the night of April 1-2 (Fig. 12). The animal stayed with a large school that moved slowly offshore, and by 2000 was over the island slope. The group then patrolled back and forth over the slope within a stretch of coast approximately 20 km in length, and over water that varied from about 360-2600 m deep. By 0300 the school and the radiotagged animal had moved closer to shore, and continued to move in ever shallower water until dawn.

Feeding schools were observed on three occasions at dusk. Each was composed of widely scattered groups, covering as much as 3 km in widest dimension, moving together. Diving was subsynchronous. Before a dive occurred groups were evident and there was much aerial behavior across the entire width of the school. Then groups of the school dove individually, all following within approximately a minute or two. Dives were long, averaging 3.5 minutes, in our records. Surfacing was approximately as coordinated as diving; that is, the various groups straggled to the surface over a minute or two.

It was striking to see these very broad diffuse schools reverse their course in relative synchrony (within a minute or two), even at dusk, indicating a communication mechanism, probably acoustic, that could pass information rather quickly across the school.

Stomach contents were obtained from four spinner dolphin caught early in the day (before noon), while three animals taken in the afternoon had empty stomachs. This same pattern seems to occur in the oceanic spinners of the tropical Pacific and a high percentage (65.2%) of empty stomachs (not segregated according to time of day) from 49 spinners taken from the eastern tropical Pacific by him, were empty (Perrin, et al. 1973). A time-stratified sample would probably show some food in stomachs in the morning before digestion of the night's catch is complete, with empty stomachs in the afternoon. If spinner dolphins were diurnal feeders one would expect few empty stomachs during the day at any time. The observed morning defecation period also fits this scheme. We conclude from our own observational data that the spinner dolphin in both the open eastern tropical Pacific and around the Hawaiian Islands feeds at night. Our evidence, and that from other studies, suggests that it feeds upon scattering-layer organisms found at considerable depth. Fitch and Brownell (1968) reach a similar conclusion from otolith studies of stomach contents of five spinner dolphins taken from the yellow-fin tuna grounds. They state: "We feel certain that three of the cetaceans we investigated (Kogia simus, Stenella longirostris, and Lissodephis borealis) had been feeding 800 feet (250 meters) or more beneath the surface. . . ." Perrin et al. (1973) similarly conclude that spinner dolphins are feeding mostly on mesopelagic fish and squid, with a small increment of epipelagic

squid species in their diet. Our results (Table 3) confirm these earlier works, but show a considerable component of sergestid crustaceans in the Hawaiian spinner diet. Epipelagic squid were absent, though common in Hawaiian waters, while such relatively deep water forms as Abralia astros-ticta and A. trigonura were common in the stomach samples but rare in collections of squid from Hawaiian waters. Dr. Richard Young (personal communication)⁴ describes the squid A. trigonura as being uncommonly taken in Hawaii, but being a vertical migrant occurring from 500 m depth during the day to the upper 100 m at night. This species made up the majority of our samples. As for A. astros-ticta, Young states that it is known in Hawaii from only a few captures, and that most were taken on the bottom in trawls, while small individuals were sometimes taken in midwater. Our samples were adults. Young comments as follows: "It is a displaced midwater faunal element, or an animal having the distinctive adaptations of a midwater animal but which seems to migrate along the bottom. The Histioteuthis is also a vertical migrator that stays below about 150 meters." (See Table 3).

John Walters comments on the shrimp Sergia fulgens that it is an enigmatic form known only in the adult form (ours were adults) from night tows.

Morning shoreward movement. After nighttime feeding, spinner schools turn toward shore, ultimately congregate in certain sheltered locations where the schools subside into the rest pattern. In the case of the radiotracked animal, this movement toward shore seemed to begin at about 0300, and to consist of a gradual movement inshore that zigzagged ever closer to shore.

The directions from which schools come into Kealakekua Bay suggests that the movement toward the coast may be a general one, and not necessarily
⁴ Dr. Richard Young, Professor of Oceanography of the University of Hawaii, examined and identified stomach samples from our Hawaiian spinner porpoises in 1973, and provided notes on the occurrence of squids in the samples, while John Walters, also of the University of Hawaii provided identifications of shrimps.

pointed precisely at a rest cove. Some entering schools first swim along the coast, round Palemano Point at the south tip of the bay, and enter the bay over the shallows near Keei and Napoopoo (see Fig. 1). Others have been noted entering the bay directly from the open sea, coming in at various angles to the trend of the coast. Still others entered from the north, once again after a traverse of unknown length along the shore to the north of the bay. More schools enter along the southern limb of the bay than from the north or center. The true figure for south entry may be even higher than the figures indicate (58% for south entry vs. 14.5% for north entry; 27.5% entered in the middle sector) since some first sightings were made close to the cliffs at the back of Kealakekua Bay, and because of their location, were placed in the second sector records. It is likely that some of these entered from the south or north prior to the beginning of observation.

These congregation patterns suggest that the bays and coves used for rest periods may not necessarily be the direct target of daily inshore movement. The bays seem simply to collect schools that accumulate along the coast after a night's feeding. The fact that more schools arrive from the south than the north may reflect the nearby presence of adequate resting areas over the rather extensive shallow water areas immediately north of the bay between Keikiwaha Point and Keauhou. Waters to the south of Kealakekua Bay are deep close to shore and only very modest sized shallow coves exist at Honaunau and Hookena. Further south, along the 20 kilometer stretch of coast between Hookena and Milolii, no spinner dolphins were seen although both flights and ship searches were made. Nonetheless, data from marked animals show movement between the populations on each side of this gap.

Unless rest areas are encountered, dolphin schools remain transient.

This does not preclude the possibility that the animals may be familiar with the various rest coves or actively seek them when nearby.

Arrival times (Fig. 13) concentrated between 0600 and 0950 hours, though some schools arrived much later in the day. The early arrivals typically subsided into rest and spent the majority of the day in the bay. Later arrivals (those entering between 1100 - 1700 hours) tended not to form resting schools and often moved out of the bay after a brief stay. The late afternoon arrivals may have completed a rest period elsewhere and then entered the bay as part of a longshore movement prior to going to the feeding grounds. Dolphins engaged in such longshore movements have been followed out to sea. In one such case a school rested, left the bay to the south, traveling slowly very close to shore until the small cove at Honaunau was encountered, and it then turned out to sea as dusk approached.

Not all dolphins schools encountering Kealakekua Bay enter it. We occasionally saw schools crossing the bay mouth and swimming on, in either direction. Our impression is that this occurred when other schools were deep in the bay, but unfortunately, adequate records to document the point were not kept. Our efforts at listening to dolphins in Kealakekua Bay showed that dolphins at the mouth of the bay can easily hear those in its deepest recesses, so the effect may be one of exclusion of the passing school by occupants. The point needs further study.

Small schools often seemed to coalesce upon arrival in the bay. This first became apparent when our estimates of school size during an arrival sequence increased sharply, or even doubled between the time the animals were at the bay entrance and when they were deeper in the bay. In other records

such obvious increase in school size occurred after the animals were deep in the bay. The arrival of such supplementary schools was occasionally observed and their coalescence into a single school noted.

School structure during entry was best observed in those that entered in the central sector, without the visual interference of headlands, or the swells and breakers that sometimes obscured sightings close to shore. Such schools were sometimes first seen as much as 4 km beyond the bay, and could be watched during the entire entry traverse. These schools typically swam in a ragged rank composed of quite discrete groups. The dolphins were often quite active, and their passage was accompanied by spins and other aerial behavior. Often, by the time the bay mouth was reached aerial behavior had subsided considerably, though it often persisted to some degree for as long as two hours after initial entry. In small schools of approximately 6-15 animals, entry was often quite unobtrusive. In spite of a conscientious watch from the cliff top during early morning hours such small schools were sometimes seen first deep in the bay. Large schools typically exhibited more aerial activity than small ones, and it appeared to persist for a longer period.

Arriving schools often come to the bows of vessels where they engage in assisted locomotion or "bowriding" (Norris and Prescott 1961). Even so, if a vessel pursued such schools, repeatedly making passes through their ranks or changing speeds upon approach, the school usually edged toward deep water, and if the harassment continued, left the bay. Observers on shipboard usually failed to note the effect on the school as a whole, since their attention was focused on the bow-riding animals. But an observer on the cliff above the bay, watching the entire school, could quickly discern this retreat.

This effect nearly always occurred, even if the intruding vessel moved very carefully. Later, when the school had subsided into quiescence, it was much more difficult to disturb the animals sufficiently to cause them to flee the bay. Even persistent attempts to enter their ranks merely caused avoidance, and often a transitory flurry of aerial activity (Fig. 14).

Defecation was a common feature of arriving schools, prior to subsidence into rest. From the underwater viewing vehicle the olive colored trails of semiliquid fecal material were often seen streaming from the porpoises. Three or four animals sometimes defecated simultaneously within the field of view of the vehicle. A rate for one 40-animal school was calculated at one defecation every 15 seconds. Presumably this rather short defecation period is related to nighttime feeding and early morning digestion. The trailing animals of a school swam through the dispersed clouds of feces with no evident reaction.

Subsidence into rest. Once a school arrived deep in Kealakekua Bay it normally subsided slowly into rest, a process sometimes requiring two hours or more. This process is so gradual and so affected by features such as school size, and the time of day, that its precise onset was difficult to assign (Fig. 14) and an arbitrary definition was necessary. Because rest involves the cessation of aerial behavior by all school members we defined rest as occurring when a ten-minute observation of the school revealed no aerial behavior. Occasionally, even this criterion was confounded because aerial behavior is, to some extent "infectious," and a school subsiding into rest may sometimes exhibit ten-minute periods without aerial behavior followed by periods in which some aerial activity occurs in several animals. But, generally, once a school was quiet for ten minutes little or no aerial

activity occurred until arousal. Typically arriving schools were ⁱⁿ ranked form, with group structure evident. Such schools often moved quickly 5-8 km/hr. and swam resolutely, with considerable aerial behavior. Little time was spent below the surface. Dives were brief (see Fig. 15). Once such a school arrived at the back of the bay, under the lava cliffs, it moved back and forth across the width of the bay. Its traverses sometimes took it nearly to Kaawaloa on the north and to Keei on the south (Fig. 1). The various classes of aerial behavior slowly disappeared in a rough graded series, the most athletic patterns such as spins and tail-over-head leaps first, then head- and backslaps, then tailslaps, and finally all but an occasional noseout was gone.

School size and shape gradually changed at the same time. The ranked school shifted into a subdiscoidal shape, and tightened markedly. For instance a school of 30 animals that once formed a spread rank over 75 meters of water might become concentrated in a 20 m diameter disc. Movements became leisurely; in fact, the surface excursions of the schools became almost surreptitious as animals rose quietly from the depths, breathed once or twice and descended again. It became very easy to overlook them, and two or three observers were needed to produce a complete record of dive sequences. During rest most time was spent underwater (Fig. 15).

Vocalization was at a high level in arriving schools and subsided as the rest period approached. Arriving schools made a variety of noises including click trains, burst-pulse signals such as squawks or barks, and pure-tone whistles or squeals. All but clicks ceased during rest.

Rest. During rest, quiet schools moved slowly back and forth, deep in the bay. Their excursions were entirely confined to shallow water (approximately 3-50 meters). Only when disturbed or when rest was over did the

schools begin to edge into deeper water. For instance, resting schools seldom ventured into the deep channel that entered the bay at Kaawaloa, but instead moved mostly back and forth between our observation station #1 and Napoopoo (Fig. 1), an area of shallow sandy bottom dotted here and there with isolated coral heads.

Resting schools often changed direction underwater, which made it difficult to predict where ^{they} would surface. Inter-individual and inter-group distance gradually decreased as rest deepened, until many animals were very close to, or actually touching one another, while the arriving school showed very evident group structure and independence of both movement and diving time within the school, the resting school swam in much closer synchrony. Arrival of synchronous diving by an entire school provided a good, if arbitrary, indicator of the onset of rest.

On a few occasions we were able to watch synchronous dives from the MOC. The underwater vantage point allowed the observer to see subgroups of animals in the school as a whole. Tight, uniformly oriented groups dove slowly, with measured tail beats, toward the sand bottom below, and levelled out a few body lengths above the bottom and moved slowly along, schooled tightly, and swam ^{largely} without individual exploratory movements. Occasionally an animal descended to the bottom and beat boils of sand up into the water with its flukes. At the end of a dive the animals rose rather steeply to the surface, not as a single tightly integrated group, but more or less seriatum, as a column of subgroups. Often after rising, the animals spread outward from this rising column a short distance before turning to define the compact confines of the surface school, like the petals of a flower opening. Once on the surface group structure could be seen, but the animals

seemed much more regularly spaced than is the case in active schools. Diving, too, was steeper and slower than in travelling groups. While individuals in resting schools seemed less alert than animals in feeding or travelling schools, the resting school itself was very wary of strange features of its environment. Any strange object placed in a rest cove, such as a buoy, boat, ^{or} line, was avoided for a matter of days before a school seemed to habituate to its presence. It was striking that they reacted to such foreign objects in much the same way as we have come to expect from fish schools, and not with typical dolphin individuality. For instance, when a resting school cruised inshore of us near the cliffs, we waited in a quietly rocking skiff some 75 meters offshore, and the school approached slowly as a discoidal group, thinned as it reached a point directly inshore of us, streamed between the skiff and the cliff as a long line of quietly moving animals, and reformed its discoidal group once past us. We found that our skiff or our anchored workboat could deform such discoidal groups from some distance, causing the side nearest the skiff to become dented or malformed as the entire school reacted to our presence. When a four hydrophone array capable of sound triangulation was placed near the path of such resting schools it was assiduously avoided and no animals were known to pass through it for six days after its placement (Watkins and Schevill 1974). A line stretched across the surface of the water was capable of deflecting such schools. In such cases, even though the animals moved slowly and other evidence of alertness such as complex phonation or aerial behavior was nearly absent, the school as a whole remained alert. We suppose this is due to sensory integration by the closely packed school, that is by the reception of environmental information by some members of a school and transmission of its occurrence to all or most of them. It was usually possible to cruise among alert schools and many individuals

might station at the bow within a few feet of an observer, but resting animals very seldom came to a vessel.

A graphic demonstration of spinner dolphins fear of strange objects was given by our attempts to encircle quiescent spinner schools with a modified Hawaiian hukilau.¹ Our hope was that this fear might be utilized to assist in their release from tuna seines, since at the time large numbers were being killed per year in the ^{yellow fin tuna} fishery. We conceived that light weight gear of this sort could be deployed in a tuna net to crowd the captive animals, and thus assist in their release. Our tests, run in August 1973, in Kealakekua Bay, used a hukilau composed of a 450 meter polypropylene cork line (1/2"; 1.27 cm) from which were hung every 2 meters thin polypropylene lines (1/4"; 0.6 cm) 18 meters in length. With this insubstantial barrier we were able to encircle whole schools of spinner dolphins in 20-40 meters of water, and to crowd them severely. In one case when the hukilau was reduced to a surface area of 6 x 10 meters, a school of 40-60 animals refused to leave through the wide openings but continued to mill inside (Fig. 16). Even when two of the thin vertical lines were removed, leaving a "door" 6 m wide, the school continued to circle, "eyeing" the opening but not passing through it. Only when the area was further reduced did the majority of animals leave through the wide opening. They had been held captive for 3 m 50 min in this fashion.

Although large and small schools may become quiescent, sporadic low intensity aerial behavior may continue. The impression given is that very

¹ A hukilau is a Hawaiian "net" made of a cork line with palm fronds roven through it at intervals, which is towed across coral areas, chasing fish in front of it. Because a mesh net is not involved it does not entangle on the rough bottom but still serves to concentrate the fish, which are then netted from inside the hukilau over sandy bottom.

small schools (ca. 6-12 animals) maintain a degree of individual wariness, perhaps related to the uncertain protective effectiveness of their few members, while very large schools may always contain some alert animals. For instance, based on a small number of observations in the large (100-150 animals) schools seen at Keahole Point, we have never noted deep quiescence. It is as if the members of the small school are afraid, and that some activity always occurred somewhere in the larger schools. Only schools of about 20-40 animals seem to achieve the most complete quiescence.

Even though aspects of diurnal behavior sequences were recorded on 83 days, complete sequences were recorded on only 13 days. Based on these observations, rest periods ranged from 41 min to 6 h (mean = 3 h 37 min).

Once quiescent, resting schools are rather difficult to disrupt. Several times cruise boats or water skiers went through resting schools during our observations. The usual result was a brief flurry of low level aerial behavior; for example, a desultory headslap, an imperfect spin, and then the school would subside into complete quiescence again (Fig. 14).

Arousal. Arousal, unlike descent into rest, is abrupt, both in terms of school dispersion and aerial activity. In a completely quiescent school arousal was marked by sudden active aerial behavior; a complete spin or headslap, for instance. Within 10 min of such initial aerial activity the school was often fully alert, with aerial activity high throughout the school. In fact, the highest levels of aerial activity recorded occurred at arousal, and later, during feeding (Fig. 14).

Zig-zag swimming. At arousal the pace of the school quickens. Group structure suddenly becomes obvious again. At arousal the school moved back

and forth across the bay, or sometimes in and out from the bay center to the cliff base. In either case the school often began to traverse deep water. Typically, it swam toward the bay mouth beginning with a flurry of activity and speed, often with animals rushing through the water, creating spray and small bow waves as they raced along. As the bay mouth was approached usually the school gradually slowed and finally began to mill; then turned back into the bay. Sometimes the school then subsided into further rest, or accelerated again, often toward the opposite side of the bay. This entire pattern is what we have termed "zig-zag" swimming. These patterns, we suspect, are to some extent influenced by the topography of Kealakekua Bay, and may take somewhat different expressions elsewhere.

Spinners were observed moving in zig-zag fashion at Kealakekua Bay, in and out and from headland to headland. The longest bout of this behavior took 2 h 45 min. Typically zig-zag swimming ended with fast swimming that took the school beyond the confines of the bay altogether. It was as if one had been rocking a blob of mercury in a bowl, and a final strong motion sent the blob flying, completely free of the bowl.

If the animals left the bay early in the day, the school usually travelled close to the shoreline, either to the north or south, and later in the day turned toward deep water offshore. When a school left the bay near dusk it usually headed directly out to sea.

As exodus from the rest location began, schools travelled either as ranked schools (wider than long), or in straggling lines arranged in more or less linear fashion. As the school moved offshore it spread. It sometimes coalesced with other schools moving in the same general direction. By the time the feeding grounds were reached, usually near dusk, a school that

during rest had formed a 25 meter diameter disc might have expanded until its groups were scattered over a kilometer or more of sea. As noted earlier, we have estimated some feeding schools as 3 km in breadth.

Social behavior, including mating, aerial behavior, sexual play and aggressive chases, becomes especially evident in spinner schools moving toward the feeding grounds. Once there subsynchronous feeding dives begin.

Dive patterns. An example of the daily cycle of dive patterns is shown in Fig. 15. As animals entered the rest area the pattern was one of short dives, with most time spent on the surface. Then this pattern gradually shifted as dives became longer and surface times shorter. When the school was near or over the shallow areas where rest occurs, dives became synchronous, or nearly so. During arrival the groups of a school, especially if it was a large one, often dive out of synchrony with one another. During rest, as shown in Fig. 15, the duration of dives continued to increase

until the longest were approximately 3:30 minutes in duration; surfacings at that time were brief--between 10 and 30 seconds duration. Throughout the rest period the school, if it is small or moderate in size, dives in synchrony. During the arousal period, surface times gradually increase while dives tend to become much more variable in length than during rest. Finally, as the school travels out to sea, individualism reaches its peak, with animals scattered in pairs, or small subgroups, or even alone, within the envelope of the school as a whole. Synchronous diving is lost as movement is at, or close to the surface, and directed into horizontal travel. Then, on the feeding grounds, when the school is at its most dispersed the scattered school slows and begins synchronized diving again, presumably to feed. Internal factors, such as the return to respiratory

equilibrium after a dive might play an important role in determining diving patterns. As for mediating signals, the cessation of aerial behavior in an area of the school that has dived could signal adjacent school segments that diving is occurring; or, ^{vocal signals} ^ could mediate it, and thus a wave of information about a dive in progress could travel across the school. The high incidence of aerial behavior in feeding schools and the lack of precise synchrony in feeding dives support such a speculation.

Social behavior. Social behavior in wild dolphin schools has thus far proved all but impossible to observe in an orderly fashion. Glimpses of individual animals or subgroups are fleeting, and the opportunity to identify individuals or their sex is sporadic. Hence, the observations that follow are highly fragmentary.

Mother-young behavior: Very small calves are always seen in the company of adults. However, young porpoises of quite small size (estimated 1.2-1.7 m total length) may form groups within a school with no evident adults in close attendance. Newborn calves with adults have been seen at all seasons of the year (Fig. 17), as have the groups of unattended larger calves.

Nursing has seldom been seen in nature. In one clifftop observation, a 60-animal school swam below, containing a group of adult-calf pairs. One of these pairs engaged in nursing. The adult turned slightly on her side as the young dolphin positioned itself obliquely alongside with its beak pressing against her at the mammary slits. The behavior persisted for a few seconds before the animals dove. The posture was like that reported in captive dolphins (Dohl, et al. 1974).

For 33 days in February - March, 1970, a female-young pair was seen in Kealakekua Bay and nearby Keauhou. Unlike most such pairs, the two often

swam near our observation vehicle. The calf had the distal 5-6 cm of its rostrum broken through and bent to the side with some ragged flesh exposed. In spite of this apparently grievous wound the calf appeared active and well nourished. Contact was very frequent between mother and calf. Both the adult and calf used their flukes, flippers and dorsal fin to achieve this contact. On two occasions the young animal touched its dorsal fin to the adult's flank, and laid its flukes up under and touching hers, and held this position as their combined tail beat propelled them both along. The young animal rode both above and below the adult, sometimes directly beneath her mid-belly, occasionally sliding backward until the moving flukes of the adult tapped against its dorsal fin. In our observations we never noted true assisted locomotion as described by Norris and Prescott (1961), though swimming speed was generally so slow that it might not be expected.

A common posture was for the baby to swim below and a little to the side of the big female, at which time she placed her flipper against the young animal's back, just anterior to its dorsal fin. Much of the time the pair in this position swam in synchrony, turning and diving together.

On occasion the young animal swung away from the adult for a few meters but soon turned, increased speed and rushed back to her. Once, during a particularly long sortie, the adult pursued the calf, slapped its back with her flukes, and then the pair dove together.

Sexual associations: At times, both on a given day and over several days time, specific subgroups of 2-6 animals, whose members could be individually recognized, were seen together from the viewing capsule. It was possible to determine the sex of some of the animals. Sexually related

behavior was exhibited between male-male and male-female pairs. It takes several forms. What Bateson (1965)¹ called "beak propulsion" was noted (Fig. 18). In it one animal swam up from below another, and inserted the tip of its rostrum into the genital slit of the upper animal, apparently pushing the passive animal along. Both the dorsal fin and the flippers are commonly used to stroke or probe the genital area of another animal, and the upper animal sometimes rode along with the dorsal fin of the lower animal pressed into its genital area. Mating postures were commonly seen, most often in alert schools early in the morning or near dusk. On one occasion (in captivity) we were able to determine that both partners in such a pair were males, even though females were present in the tank. We were able to confirm heterosexual contact in some pairs in nature. Typically, one animal swam in the normal upright orientation while another swam upside down, with the genital areas of the two pressed together. Either sex could be above or below. Intromission was usually difficult to see, but was noted on occasion. Contact was sometimes maintained for several seconds. In some observations the upper partner was relatively quiescent, and propelled itself with fluke strokes of much reduced amplitude compared to those of normal swimming. One mating chase was noted as a school moved onto the feeding grounds off Keauhou, the pair raced by the bow of our vessel as we travelled at an estimated 4 knots. They dove and spiralled swiftly together. The coupling and synchrony of movement of the pair was so perfect that two animals were not evident until the pair turned on its side. Together they veered away from the bow, diving an estimated 20 m down, and remaining in the coupled position for several seconds. After one such union, one member of the pair was noted to leap in a particularly violent

¹Bateson, G. (1965) The cetacean community in Whaler's Cove-Sea Life Park. Rep. Career Devel. Award (K3-NH-21, 931) Nat. Inst. Health (mimeo). Parts of this work also appeared in McIntyre, J. Mind in the Waters,

spin, followed by two additional spins of lesser intensity. We heard whistling with the unaided ear when such coupled animals were near the ship.

A particularly complete observation of mating was made from the MOC on July 26, 1970, at Kealakekua Bay. A male-female pair swam directly in front of the viewing capsule, and the female swung under the male until their ventral surfaces were in contact. The penis of the male was seen to enter the female, though no thrusts were noted as the position was held for 3-5 seconds, while the animals glided without fluke strokes, and then the animals parted. Shortly, the female again moved under the male but no further intromission appeared to take place. Instead, the male accelerated with a few fluke strokes, and the pair cruised off, side by side.

Competition for partners was occasionally observed. On March 29, 1970, at Kealakekua Bay, the MOC entered a school of 12-13 animals, and two were noted swimming upside down. Both pursued and came up under a single adult above them. Later, three inverted animals pursued two in the normal swimming posture. At that moment another large adult swam rapidly to the moving group and forcefully inserted itself between one inverted animal and the one above it. The upper animal then dove away from the group, with the intruder following. The two inverted animals moved quietly, maintaining their upside-down orientation, toward another nearby animal swimming in normal orientation.

Observations of captive spinner dolphins show that much social interaction is sexually related, and that it may occur between animals of all age classes and combinations of both sexes. As has been found in the Atlantic bottlenose dolphin (Tursiops truncatus) sexual behavior and social communication are interwoven to such an extent that it is often impossible, to separate true courtship and mating behavior from communicative behavior of other sorts. For example, Caldwell and Caldwell (1967) reported a 2-day

old male Atlantic bottlenose dolphin having an erection when brushed by its mother. Sexual maturity isn't reached in the spinner dolphin until a minimum of 3.7 years (Perrin, et al 1976)¹ 1976) and even later in the bottlenose dolphin and thus one must view this precocious use of sexual patterns as part of the development of communication concerning relationship. Such communicative use of sexual patterns has been reported for mixed schools of captive spinner and spotted dolphin (S. attenuata) (Bateson 1965).

Other Social Patterns. Contact, not necessarily sexual in context, is common between members of dolphin schools. When groups of animals swam near the viewing capsule one could often see animals touching one another with the tips of pectoral fins, the dorsal fins or fluke tips. Jostling or pushing of animals near the capsule often occurred and was accompanied by sound emissions. Such jostling can be seen commonly in other bow-riding groups. Because a few animals from a given school seem to do most of the riding, and some seem to occupy specific places at the bow, one gains the impression that hierarchical relations in the school are involved.

The release of air may correlate with social signals in spinner schools. Commonly, long streams of air were noted issuing from the blowhole corners in spinners near the capsule. Whistles and chirps could often be heard concurrently. Sometimes, during active chases one or more animals would release a large bubble of air underwater, which boiled upward to the surface. Pryor (1973) has correlated such behavior in captive animals with frustration.

Spinner dolphins change school swimming patterns in relation to weather. In rough seas, groups of dolphins appear to ride the swells and breaking

waves that sweep toward the Kona coast. On one such occasion, while we
¹Perrin, W.F., D.B. Holts and R.B. Miller 1976. Growth and reproduction of the eastern spinner dolphin. A geographical from of Stenella longirostris in the eastern tropical Pacific. U.S. Dep. Commer., NOAA, NMFS, Admin Rep., LJ-76-13, 84 pp.

"hove to" in a rough sea, perhaps 100 spinners passed us. They were divided into small groups of less than a dozen animals. These groups swam tightly together, and often could be seen racing down the foreslope of waves, sometimes breaking the water together, and sometimes staying wholly within the wave. Such behavior is commonly seen in other cetacean species (Norris and Dohl in press).

Sound emissions. A detailed study of spinner dolphin sound emissions will be presented in a future paper. A few observations are appropriate here.

There is a marked diurnal fluctuation in the kind and amount of spinner dolphin vocalization (see also Powell 1967). Alert schools produce an array of sound types such as clicks, pure-tone whistles or "squeals" and a variety of burst pulse signals that can be described by such terms as barks, moos, chirps, etc. The clicks are of considerably lower intensity than either the whistles or the burst pulse signals (Watkins and Schevill 1974) and the clicks may be more tightly focused.

Resting schools are nearly silent, emitting almost entirely clicks and even these are sporadic. Simultaneous with arousal, vocalizations rise in variety and abundance. Whistles and burst pulse signals can be heard quite long distances underwater. With Watkins and Schevill, we were able to station ourselves outside Kealakekua Bay and hear whistles and various burst pulse signals from a group of spinners swimming close to the cliff, approximately two kilometers distant. Thus a school of dolphins swimming outside Kealakekua Bay during longshore movement would be able to detect animals deep in the bay without entering it. It is possible that the schools we have seen passing the bay when others occupied it may have been excluded by acoustic signals.

No context-specific sound signals have been identified by us, except that it seemed clear that clicks were emitted concurrent with the inspection of the environment. The likelihood of context-specific acoustic signalling in the daily events in the school, however, seemed high. For example, synchronous diving in very widely dispersed schools, or simultaneous turning of an entire school at dusk, are unlikely to be visually cued (though it is not impossible). The sounds produced by aerial behavior have in a few instances, been picked up by our listening gear. Tail slaps are especially loud, while spins (which we have recorded in captive situations) produce a lower intensity signal quite different in character.

Predators. Hawaiian spinner dolphins seem to be attacked with some frequency by sharks. Several of the scarred animals we catalogued had obviously been wounded by large sharks. Lunate rows of tooth marks, especially on the tail region, some apparently from sharks with a 12-15" gape, were noted. In one case it seemed that the entire tailstock had once been in a shark's mouth. Nicked or tattered dorsal fins may also have been produced by shark bite.

Subcircular scars somewhat larger than a silver dollar commonly seen on tropical and subtropical cetaceans are common on spinner dolphins. Jones (1971) has suggested that these scars are produced by the small squaloid shark Isistius brasiliensis. This small shark occurs with scattering layer organisms, is bioluminescent over its entire body, and is thought to be a squid mimic. Feeding dolphins may be attracted to it, and when close, the shark may swim to the dolphin, attach itself, and then scoop out a disc of blubber and flesh with its peculiar dental and branchiostegal apparatus. The shark has erect ^{cutting} teeth only in the lower jaw, and a

jaw apparatus that allows it to attach and push the teeth through the flesh of its prey like a cookie cutter. The shark may bite while facing the tail of the porpoise and be swung around in the current, cutting as it goes. Discs of dolphin blubber have been found in the stomachs of this shark (Jones 1971). We have seen fresh wounds of this shape and size several times, including some completely through the blubber to the flesh beneath. Nearly every adult dolphin bears some scars of this sort, on some part of its body. We have never seen such scars on the appendages or head, though they are common on the throat, flanks, and especially on the belly and the region between the flippers.

Discussion

Instead of finding tightly knit schools of constant size that habitually occupied a given cove, as we had expected we found coves occupied by schools of highly variable numbers and composition. These variable schools often merged with other schools to form large feeding groups offshore, and school members moved back and forth between resting areas many kilometers apart in what seemed a completely free fashion. Rather than finding dolphins occupying a "home cove," the tendency to gather in shallow waters near shore seems to be related to a combination of topographic factors including the presence of adequate areas of shallow water, and proximity to nearby deepwater feeding grounds. Further, the population occupying such a cove during the daily rest period seems limited in some fashion by this same topography. Kealakekua Bay seems able to hold only about 60-70 animals, and even this number seems so large that rest may be inhibited. Deep rest, without aerial behavior, seems only to occur when relatively few animals, about 30-40 or less, are in the cove. In contrast, Keahole Point regularly holds more than 100 animals during daily rest.

Instead of finding schools headed directly for rest areas in the morning, we found schools moving toward the coast in the morning in a much more general fashion, encountering the coast, swimming alongshore, entering coves, sometimes coalescing with schools already in occupancy, or apparently sometimes passing by a cove filled with animals, to move on toward other less occupied rest areas. The entry and exit patterns of schools relative to coves also suggests such opportunistic use. At Kealakekua Bay schools entered primarily from the south perhaps because rest areas south of this bay are very restricted while much more extensive areas exist to the north and in effect this inhospitable shore "collects" but does not hold incoming schools. Exit, on the other hand, is primarily to the north, as if schools came into the cove, rested for a time, and continued on their way toward offshore feeding grounds. The primary feeding grounds seem to be to the north and west of Kealakekua Bay, off the shallows of the island, though our observations are sparse. To the north of Kealakekua Bay are other rest areas, while to the south deep water adjoins the shore. Thus occupancy or lack of same of a given rest cove and arrival direction to it may be related to nighttime feeding movements which leave animals offshore at various locations after the scattering layer descends with dawn. None of this, of course, indicates that dolphins do not know where available rest areas are, or know features of them.

What, then, is the true dolphin school? Are the large offshore aggregations, formed of a coalescence of smaller resting groups, such a cohesive unit? Or, should we focus our attention on school subgroups of a few animals, which may habitually swim together (though our evidence is inconclusive in this respect), in the search for structure, regarding the

large groups as opportunistic assemblages? Or, can both be properly considered as schools?

The large offshore feeding assemblages have clear structure in some respects. Such schools often dive and surface more or less together, and much social behavior is evident at times in them. These schools swim in a common direction and sometimes change course in a coordinated fashion. We often noted age-related subgroups within them; mothers and calves, or juveniles swimming together. But, if such schools are followed they will sometimes split into parts that move in different directions, and clearly, they fragment during the day when smaller schools enter coves or shallows to rest.

Smaller schools exhibit most of the same behavior, though many times not all age classes will be represented in them. Schools of less than about 30 animals are seldom split for long by a vessel. These groupings we call schools, preferring to recognize that such schools change in size from time to time.

Clearly, from our marked animal information, individuals utilize a rather extensive area of coast for feeding, moving from group to group, and thus, in aggregate the population of a given portion of coast is a functional unit, in relation to its trophic relations with the immediate environment. The degree of discreteness of such populations from those adjacent remains wholly unknown, as does any possible intermixing between islands.

Considering this high degree of fluidity, how is directed movement of a school achieved, and how does the structure of schools come about? No leader seems to exist in the standard sense of an animal determining direction of movement by swimming at the head of a group. Yet directed movement does

occur in cetacean schools. Killer whales arrive off sea lion and sea elephant rookeries at the proper time to catch pups (Norris and Prescott 1961), and pilot whales arrive at specific feeding grounds when squid come to spawn, or when capelin arrive in large schools (Sergeant and Fisher 1957). Such patterns presumably have a learned component, and similar patterns of dolphins opportunistically using human activities to locate and capture food must be largely or wholly learned. For instance, bottlenose dolphins follow trawlers in both the Gulf of Mexico (Leatherwood 1975) and in the Gulf of California (Norris and Prescott 1961) and obtain fish and other food items stirred up by the trawl or cast over the side during sorting of the catch.

Tavolga and Essapian (1957) describe adult male bottlenose dolphins harassing newborn calves and their mothers, and dominance by adult females is also discussed. We have noted strong aggressive behavior in captive male spinner dolphins at Sea Life Park oceanarium in Hawaii. In the wild

school similar actions probably serve to order the structure of the school. Females and newborn young may be herded to their normal position in the interior of the school. We expect that such aggression combined with experience may serve to regulate the direction of school movement from various locations in a school. For instance, adult male killer whales usually occupy a position in travelling schools far out on the wings of the moving group, and from this position directional signals may be communicated to the school as a whole (Norris and Dohl in press).

The tendency of spinners to rest over shallow sandy areas is most probably a protective adaptation allowing the quiescent school to place a protective bottom close beneath it, and a shore nearby on one flank. The chances of attack from those directions by large deep water sharks are

correspondingly reduced. With much individual behavioral flexibility suppressed in resting schools, collective wariness rises, we presume through sensory integration by the school. Thus, the use by spinners of alert daytime-feeding spotted dolphin (Stenella attenuata) schools in the open eastern tropical Pacific Ocean, we feel, may account for the otherwise unusual daytime association between these two species.

We regard this study as preliminary, allowing glimpses into the life of one wild dolphin species, and focusing our attention on important problem areas such as acoustic signalling, school structure, energetics, and social relationships.

Acknowledgements

The assistance we have been given in this study has been great. We thank our vessel captains, Dan Camacho, Frank Cunningham, Georges Gilbert, Roger Gray, George Hanawahini, and Vern Hanson, and also our observers, Larry Hobbs and David Bryant.

We thank William Arbeit, George Barlow, Marlee Breese, Gregory Bateson, Paul Breese, Robert Elsner, William Evans, Sheri Gish, Sharon Gwinn, Ted Hobson, Ingrid Kang, William McFarland, Fred Munz, Karen Pryor, Scott Rutherford, William Schevill, Robert Shallenberger, Edward Shallenberger, and William Watkins for other field assistance.

The discussions we have had with George Barlow, Gregory Bateson, William Perrin, William Rogers, and Karen Pryor have helped a good deal to clarify our ideas of what these often elusive and hard-to-see animals were doing.

Sherwood Greenwell went far out of his way helping with our observation posts on his land. Bob Haws and Don Brandy, especially, helped with the flying. Tap Pryor assisted us many times with ships and support. The {MOC} grew from the hands and mind of Jimmy Okudara.

Richard Young and John Walter, of the University of Hawaii identified the cephalopod and shrimp remains in stomach contents.

Nothing could have been accomplished without patient programmatic support, most of which came from the Biological Branch of the Office of Naval Research, through the continuing interest of Deane Holt, Helen Hayes, Charles Woodhouse, and Ron Tipper. Other support (for the

hukilau work) came from the National Marine Fisheries Service, and from the Oceanic Institute.

Finally, our thanks to Bob Leslie, native of Kealahakua Bay, and some of his fishermen associates, such as "Only LeRoy," we learned much about our animals and the place where they lived.

Literature Cited

- Caldwell, M.C., and D.K. Caldwell. 1967. Dolphin community life. Los Ang. ~~Cy.~~ Mus. Quarterly 5(4): 12-15.
- Dohl, T.P., K.S. Norris, and I. Kang. 1974. A porpoise hybrid: Tursiops x Steno. J. Mammal. 55(2): 217-221.
- Evans, W.E. 1973. Echolocation by marine delphinids and one species of freshwater dolphin. J. Acoust. Soc. Am. 54(2): 191-199.
- Evans, W.E. 1974. Radio-telemetric studies of two species of small odontocete cetaceans. In W.E. Schevill (editor) ^{the} ~~the~~ Whale Problem. A status report, ~~G.C. Ray and K.S. Norris, consult. eds.~~ Harvard Univ. Press, Cambridge, Mass. 385-394.
- Fitch, J.E., and R.L. Brownell, Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board. Can. 25: 2561-2574.

- Hester, F.[#]J., J.[#]R. Hunter, and R.[#]R. Whitney. 1963. Jumping and spinning behavior in the spinner porpoise. J. Mammal. 44(7[#]):586-587.
- Jones, E.[#]D. 1971. Isistius brasiliensis, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull., U.S. 64(4[#]):791-798.
- Kasuya, T. 1972. Growth and reproduction of Stenella coeruleoalba based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst. Tokyo 24:57-59.
- Kasuya, T., N. Miyazaki, and W.[#]H. Dawbin. 1974. Growth and reproduction of Stenella in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. Tokyo 24:157-226.
- Leatherwood, J.[#]S. 1975. Some observations of feeding behavior of bottle-nosed dolphins (Tursiops truncatus) in the northern Gulf of Mexico and (Tursiops cf. T. gilli) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.
- McBride, A.[#]F., and D.[#]O. Hebb. 1948. Behavior of the captive bottle-nosed dolphin, Tursiops truncatus. J. Comp. and Physiol. Psychol. 41:111-123.
- Norris, K.[#]S., and J.[#]H. Prescott. 1961. Observations of Pacific cetaceans in Californian and Mexican waters. Univ. Calif. Publ. Zool. 63(4):291-402.

Norris, K.[#]S., and W.[#]E. Evans. 1967. Directionality of echolocation clicks in the rough-tooth porpoise Steno bredanensis (Lesson). In W.[#]N. Tavolga, (editor), Marine ^{bio}acoustics, 305-316.

Norris, K.[#]S., and T.[#]P. Dohl. In press. The structure and functions of cetacean schools. In The Behavior of Marine Mammals, L. Herman (ed.), Wiley Interscience.

Perrin, W.[#]F. 1972. Color patterns of spinner porpoises (Stenella cf. S. longirostris) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish.. Bull., U.S. 70: 983-1003.

Perrin, W.F. 1975. Variation of spotted and spinner porpoises (genus Stenella) in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr., Univ. Calif. San Diego 21: 1-206.

Perrin, W.[#]F., R.[#]W. Warner, C.[#]L. Fiscus, and D.[#]B. Holts. 1973. Stomach contents of porpoise, Stenella spp. and yellowfin tuna, Thunnus albacares, in mixed-species aggregations. Fish.. Bull., U.S. ⁷¹ 1077-1092.
1092.

- Powell, B.A.[#] 1976. Periodicity of vocal activity of captive Atlantic bottlenose dolphins: Tursiops truncatus. Naval Ordnance Test Station. Tech. Publ. 4302: 237-244.
- Pryor, K.W.[#] 1973. Behavior and learning in porpoises and whales. *Naturwissenschaften* 60: 412-420.
- Saayman, G.S.[#], and C.K.[#] Tayler. 1971. Responses of man to captive and free-ranging cetaceans. *Baralugia*; Proc. 1st and 2nd So. African Symp. for Underwater Sciences. Univ. Pretoria, pp. 1-9.
- Saayman, G.S.[#], D. Bower, and C.K.[#] Tayler. 1972. Observations on inshore and pelagic dolphins on the southeastern Cape coast of South Africa. *Koedoe* 15: 1-24.
- Saayman, G.S.[#], C.K.[#] Tayler, and D. Bower. 1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (Tursiops aduncus Ehrenburg). *Behavior* 44(3-4): 212-233.
- Saayman, G.S.[#], and C.K.[#] Tayler. In press. The socioecology of humpback dolphins (Sousa sp.) In The Natural History of Whales, H.E.[#] Winn and B.L.[#] Olla (ed.), Plenum Press, New York.
- Schevill, W.E.[#], and W.A.[#] Watkins. 1966. Sound structure and directionality in Orcinus (killer whale). *Zoological* 51(2): 71-76.
- Schlegel, H. 1841. *Abhandlungen aus dem Gebiete der Zoologie und vergleichenden Anatomie*. 1. Heft. A. Arnz and Comp., Leiden, 44 pp.
- Sergeant, D.E.[#], and H.D.[#] Fisher. 1957. The smaller cetacea of eastern Canadian waters. *J. Fish. Res. Board Can.* 14(1): 83-115.
- Shane, S.H.[#] 1977. The population biology of the Atlantic bottlenose dolphin, Tursiops truncatus, in the Aransas Pass area of Texas. Masters thesis, University of Texas.

- Tavolga, W.[#]N., and F. Essapian. 1957. The behavior of the bottle-nosed dolphin (Tursiops truncatus); mating, pregnancy, parturition, and mother-infant behavior. Zoologica 24(2): 11-31.
- Tayler, C.[#]K., and G.[#]S. Saayman. 1972. The social organization and behavior of dolphins (Tursiops aduncus) and baboons (Papio ursinus): some comparisons and assessments. ^{Prov.?}Ann. Cape. Rev. Mus. Nat. Hist. 9: 11-49.
- Watkins, W.[#]A. and W.[#]E. Schevill. 1974. Listening to Hawaiian spinner porpoises, Stenella cf. Longirostris, with a t ee-dimensional hydrophone array. J. Mammal. 55(2): 319-328.
- Wells, R.[#]S., B. Irvine,[#] and M.[#]D. Scott. In press. The social ecology of Atlantic bottlenosed dolphins off Florida's west coast: A comparison with other inshore odontocetes. In L. Herman (editor), The Behavior of Dolphins. Wiley Interscience.
- Würsig, B., and M. Würsig. 1977. The photographic determination of group size, composition and stability of coastal porpoises (Tursiops truncatus). ^(Wash., D.C.)Science 198: 755-756.
- Würsig, B. 1978. On the behavior and ecology of dusky and bottlenose porpoises in the south Atlantic. Ph.D. Thesis, State Univ. of New York, Stony Brook, N.Y. 334 pp.

Table Captions

- Table 1. Movement of spinner dolphins identified by natural scars and marks. On six occasions individual animals were seen at one location, moved to another, and then returned to the first. Three individuals were seen only at one location, though they did not remain resident there. On three occasions individuals were seen at two or more locations on consecutive days.
- Table 2. Occurrence of a single spinner dolphin (No. 24) and its school size at Kealahou Bay, Hawaii, in 1970.
- Table 3. Squid and shrimp in the diet of Hawaiian spinner dolphins.

Table 1. ^I/_M Movement of Hawaiian spinner dolphins that were identified by natural scars and marks.

<u>Porpoise number</u>	<u>Total time observed (days)</u>	<u>Maximum distance travelled</u>	<u>Number of sightings</u>
1	293	18 km	3
23	183	0 km	3
24	1,096	36 km	14
30	342	36 km	11
32	246	0 km	3
39	236	36 km	3
40	275	36 km	4
44	170	36 km	6
45	1,220	113 km	7
46	862	10 km	3
49	39	36 km	2
50	1	0 km	1

Reversals = 6

One location = 3

Two or more sequential locations = 3

Table 2. [/]_M Occurrence of a single spinner dolphin (No. 24) and the size of schools in which it was seen at Kealakekua Bay, Hawaii.

<u>Dates of observation</u>	<u>Estimated School sizes</u>	<u>Number of times seen</u>
28 Apr. 1 - 16 May 1970	15-30	3 days of 9
23 June - 30 June 1970	15-40	2 days of 8
10 Sept. - 18 Sept. 1970	25-36	3 days of 9
28 Oct. - 6 Nov. 1970	7-120	3 days of 10

Table 3. Squid and shrimp in the diet of Hawaiian spinner dolphins.

Sample and date	Capture locality	Squid		Shrimp
0170-42 Sept. 24/70	1 km off Ala Wai, Oahu	28 mantles (mantle length 25-52 mm, mean 38.9 mm)		11 <u>Pasiphaeids</u> (to 17.8 mm carapace length)
		5 <u>Abralia astrosticta</u>		1 small
		14 <u>Abralia trigonura</u>		4 abdominal portions
		67 squid beaks, probably of the same species		1 Caridean cephalothorax
				Probable <u>Euphausiid</u> fragments
0170-35 Mar. 25/70	Off Waikiki, Oahu	2 <u>Abralia astrosticta</u>		No identifiable remains
		7 <u>Abralia trigonura</u>		
		152 squid beaks of above species		
		49 macerated squid		20 <u>Sergia fulgens</u> (12.5-15.5 mm carapace length, mean 14.6 mm)
0171-1 Jan. 8/71	200 m off Kailua-Kona Harbor, Hawaii	2 <u>Abralia astrosticta</u>		
		6 <u>Abralia trigonura</u>		
		204 squid beaks, probably of the above species		
		1 <u>Histioteuthis</u>		

Table 3 (Continued)

Sample and date	Capture locality	Squid		Shrimp	
OI71-2 Jan. 8/71	200 m off Kailua-Kona Harbor, Hawaii	2	<u>Abrolia astrodicta</u>	1	<u>Acanthephyra</u> sp.
		8	<u>Abrolia trigonura</u>	1	<u>Pasiphaea</u> sp.
		310	squid beaks of the above species	2	<u>Pasiphaea</u> sp.
				15	<u>Sergia fulgens</u> (12-14.5 mm mean 13.6 mm. Some of the above may be of undetermined species)
				1	<u>Oplophorus grimaldii</u> (iden- tification probable)
				3	<u>Acanthephyra</u> sp. (identifica- tion probable)

Figure Captions

Figure 1. $\frac{1}{M}$ Kealahou Bay, Hawaii. Shown are observation posts on cliff that backs the bay, shallow water areas (in meters), and approximate areas frequented by resting schools of spinner dolphins. Also indicated are arbitrary bay sectors used in analysis of arrival and departure directions.

Figure 2. -- Hawaiian spinner dolphin. Drawing courtesy William Perrin.

Figure 3. $\frac{1}{M}$ Mobile Observation Chamber (MOC) at Kealahou Bay. The hatch is open to a cylindrical observation chamber that projects 1.5 m below the hull. The observer views through a 360° band of plexiglas windows. The operator, steers and operates the engine.

Figure 4. $\frac{1}{M}$ Sightings of spinner dolphin schools by the authors (triangles) in the Hawaiian Island chain.

Figure 5. $\frac{1}{M}$ Spinner dolphin with vertical white stripe on both sides of its dorsal fin. We suspect that this animal had shed a radio pack after the pin had migrated out of the fin.

Figure 6. $\frac{1}{M}$ Spinner dolphin reentering the water after a spin, seen from below. Note the longitudinal hollow of water scooped out by the rotating animal. Photo by Henry Groskinsky, courtesy Time Inc.

Figure 7. $\frac{1}{M}$ Body postures of spinner dolphins during a spin. Vertical and horizontal dimensions of leap not to scale. Redrawn from Hester et al. (1963).

Figure 8. The tail-over-head leap of a spinner dolphin. This may, at times, be combined with a spin.

Figure 9. A typical backslap of a spinner dolphin. As the school moves slowly the porpoise emerges in the direction of swimming, belly up, and arches its back at the last instant and slaps its back against the water.

Figure 10. A headslap. The spinner dolphin emerges belly down in the direction of swimming and flexes its body forward sharply at reentry.

Figure 11. An inverted tailslap by a spinner dolphin. Tailslaps also may be made in normal body posture. Often a series of a dozen or more slaps may be made at a single time, which has been termed "motorboating" because of the white wake and the sound produced.

Figure 12. Radiotrack chart of a marked spinner dolphin, [March 31] - [April 2] 1971. Dolphin stayed in moving school of 100 animals presumably feeding over the island's submarine slopes.

Figure 13. Cumulative record of time of first sighting, onset of rest, wakening, etc.

Figure 14. Aerial behavior per 10-minute interval for a spinner dolphin school of approximately 40 animals, [June 30] 1971 Kealakekua Bay, Hawaii. Synchronous dives define the period, broken briefly by the speedboat. See text.

Figure 15. Trends in diving and surface times in a 40 animal school of spinner dolphins, Kealakekua Bay, Hawaii, [May 2] 1970. Breaks in record represent loss of the school by the observer, when a surfacing and descent was apparently missed.

Figure 16. An Hawaiian "hukilau" composed of a cork line and hinging vertical weighted lines, showing a school of spinner dolphins held inside. Vertical lines are

3 m apart and 20 m long. See text.

Figure 17. Annual occurrence of newborn in spinner dolphin schools off Hawaii (1968-72). Only sightings of newborn with evident fetal folds are included.

Figure 18. Beak propulsion by a captive pair of spinner dolphins at Sea Life Park, Hawaii. An adult female is pushing an adult male.

DISTRIBUTION LIST

Director, Defense Research & Engineering
Office, Secretary of Defense
Washington, D.C. 20301
ATTN: Office Assistant Director(Research)

Office of Naval Research
Arlington, Va. 22217
ATTN: (Code 480)

Office of Naval Research
Branch Office
1030 E. Green Street
Pasadena, Calif. 91106

National Oceanographic Data Center
NOAA
3300 Whitehaven Street N.W.
Washington, D.C. 20235

Defense Documentation Center
Cameron Station
Alexandria, Va. 22314

CO NORDA
NSTL Station
Ms. 39529

Director
Office of Naval Research Detachment
NSTL Station
MS 39529
ATTN: (Ron Tipper)